A synthesis of major environmental body size clines of the sexes within arthropod species

Curtis R. Horne[a]*, Andrew G. Hirst[a,b]* and David Atkinson[c]

[a]School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP, United Kingdom.

[b]Centre for Ocean Life, National Institute for Aquatic Resources, Technical University of Denmark, Kavalergården 6, 2920, Charlottenlund, Denmark

[c]Institute of Integrative Biology, University of Liverpool, Liverpool, L69 7ZB, United Kingdom.

*Co-first authors (authors contributed equally to this work).

Corresponding author: Andrew G. Hirst (aghirst@liverpool.ac.uk)

Author Contributions

CRH, AGH and DA designed the study and wrote the paper. CRH collected the data and performed the statistical analyses.

ABSTRACT

Body size at maturity often varies with environmental conditions, as well as between males and females within a species (termed Sexual Size Dimorphism (SSD)). Variation in body size-clines between the sexes can determine the degree to which SSD varies across environmental gradients. We use a meta-analytic approach to investigate whether major biogeographical and temporal (intra-annually across seasons) body size-clines differ systematically between the sexes in arthropods. We consider 329 intra-specific environmental gradients in adult body size across latitude, altitude and with seasonal temperature variation, representing 126 arthropod species from 16 taxonomic orders. On average, we observe greater variability in male than female body size across latitude, consistent with the hypothesis that, over evolutionary time, directional selection has acted more strongly on male than female size. In contrast, neither sex exhibits consistently greater proportional changes in body size than the other sex across altitudinal or seasonal gradients, akin to earlier findings for plastic temperature-size responses measured in the laboratory. Variation in the degree to which body size gradients differ between the sexes cannot be explained by a range of potentially influential factors, including environment type (aquatic vs. terrestrial), voltinism, mean species' body size, degree of SSD, or gradient direction. Ultimately, if we are to make better sense of the patterns (or lack thereof) in SSD across environmental gradients, we require a more detailed understanding of the underlying selective pressures driving clines in body size. Such understanding will provide a more comprehensive hypothesis-driven approach to explaining biogeographical and temporal variation in SSD.

Keywords: Sexual Size Dimorphism, Biogeography, Temperature, Seasonality, Altitude

INTRODUCTION

Sexual size dimorphism (SSD) characterises the degree to which males and females differ in size within a species. Body size differences between the sexes have been related to dimorphic behavioural and ecological characteristics. For example, males are commonly larger than conspecific females in many endothermic vertebrates, especially those in which males compete with each other and hold territory or resources (e.g. Owens & Hartley, 1998; Soulsbury *et al.*, 2014). By contrast, in many ectothermic invertebrate species, including arthropods, the female is often the larger sex (e.g. Fairbairn, 1997; Blanckenhorn *et al.*, 2007a; Teder, 2014). The larger body size of females in comparison to conspecific males has been attributed to their greater energy investment in the production and care of offspring, and the positive correlation between body size and fecundity (Slatkin, 1984; Hedrick & Temeles, 1989). Males invest relatively less energy in the production of gametes and often less in the care of offspring too; thus, males being larger may not result in an increased ability to produce more or fitter offspring. However, males maturing at a smaller size as a result of more rapid development could have a distinct advantage when the juvenile period is associated with high mortality rates, as may occur when males undertake risky mate-searching behaviour (Vollrath & Parker, 1992; Savalli & Fox, 1998; Blanckenhorn, 2000; Kiørboe & Hirst, 2008). Earlier maturation in males also means they are ready to mate with sexually maturing females - opportunities that later maturing males may miss (Wiklund & Fagerström, 1977).

Variation in size at maturity within a species is affected by a range of environmental conditions. Such size variation can result from phenotypic plasticity, but also includes variation across populations, as observed across latitudinal gradients. Several biogeographic and biological 'rules' have consequently been proposed to describe systematic variation in body size. These include size clines over latitude, altitude, and with temperature and resource availability (Bergmann, 1847; Atkinson, 1994; Partridge & Coyne, 1997; Blanckenhorn & Demont, 2004; Chown & Gaston, 2010; Forster *et al.*, 2012; Shelomi, 2012; Horne *et al.*, 2015; Horne *et al.*,

2017; Horne *et al.*, 2018). The extent to which these body size-clines differ between the sexes will determine the degree to which SSD varies across environmental gradients. Yet, very few studies have investigated sex-based variation in intra-specific adult body size clines, particularly across biogeographical and seasonal gradients. Latitudinal clines in body size have previously been compared between males and females in vertebrates and invertebrates, although the different metrics used to quantify variation in SSD resulted in contrasting outcomes. Males were the more variable sex when the ratios of sex-specific latitudinal slopes were compared (i.e. the relative difference between male and female latitudinal body size gradients), but neither sex was more variable when reduced major axis (RMA) slopes of male size on female size were used (Blanckenhorn *et al.*, 2006). Variation in SSD across latitudinal-size (L-S) gradients, altitudinal-size (A-S) gradients, and with intra-annual temperature variation in the field therefore requires further investigation. Such analyses are necessary if we are to better understand sex-based differences in responses to the environment, as well as the likely reasons for changes in size at maturity. The need to understand environmental effects on size at maturity and SSD has been highlighted in a recent debate on the extent to which constraints on growth *versus* the allometric scaling of costly reproductive output drives mature size and SSD (Barneche *et al.*, 2018; Marshall & White, 2018; Kearney, 2019; Marshall & White, 2019; Pauly, 2019).

This study focuses on species of arthropod. Arthropoda is the most species-diverse phylum, which often dominates metazoan communities numerically in both aquatic (e.g. crustaceans) and terrestrial systems (e.g. insects) (Zhang, 2013). Consequently, they form key food web components and can play an important role in the biogeochemical transformation of ecosystem materials (Turner, 2004; Losey & Vaughan, 2006). Changes in size at maturity in the field observed across latitude, altitude, and with seasonal temperature change (in this last case considering only multivoltine species), were recently synthesized for arthropod species (Horne *et al.*, 2015; Horne *et al.*, 2017; Horne *et al.*, 2018). These studies revealed similarities

in both the direction and magnitude of some of these major body size gradients, as well as consistency in the responses of certain taxa and between aquatic and terrestrial habitats (Forster *et al.*, 2012; Horne *et al.*, 2015; Horne *et al.*, 2017). However, a detailed exploration of how these clines differed between males and females was not undertaken. The present study provides an opportunity to test the degree to which body size responses vary between the sexes across each of these major environmental gradients.

Effects of resource availability, juvenile density, and rearing temperature on variation in SSD in arthropods have previously been examined in short-term laboratory experiments (Teder & Tammaru, 2005; Stillwell *et al.*, 2010; Hirst *et al.*, 2015; Rohner *et al.*, 2018). However, where sex differences in body size plasticity have been observed, the underlying mechanisms and selective pressures are poorly understood. Changes in juvenile density and food quantity or quality have produced greater female size plasticity within arthropod species (Stillwell *et al.*, 2010), many of which exhibit female-biased SSD, and thus the relative contribution of sex versus body size to the degree of size plasticity is difficult to distinguish. A more recent study, which investigated sex-specific body size plasticity under laboratory conditions in holometabolous insects, found that the larger sex generally exhibited greater plasticity in response to environmental factors (including food quantity and temperature), indicating that selection on size, rather than on reproductive role, may be an important driver of sex-specific plasticity in insects (Rohner *et al.*, 2018). These outcomes suggest that the energetic restrictions affecting body size plasticity may be acting to a greater extent on larger bodies. In contrast, a meta-analysis that included both aquatic and terrestrial arthropods found that laboratory temperature-size (T-S) responses did not vary systematically between the sexes (Hirst *et al.*, 2015). These different outcomes suggest that there is generally a sex-dependent effect of food resources, but not temperature, on body size. Given the large number of environmental parameters that can vary in the field (including both resource availability and temperature), it is difficult to predict whether the degree of SSD will vary systematically across

biogeographical and temporal gradients. Thus, in the present study we aim to establish whether:

i) Females exhibit the greatest proportional changes in body size across latitude, altitude, and with seasonal warming.

ii) The larger sex exhibits the greatest proportional changes in body size across latitude, altitude, and with seasonal warming.

iii) Neither of the sexes exhibits consistently greater proportional changes in body size than the other sex across these major environmental gradients.

We also investigate the degree to which any differences in these body size gradients between males and females within species depends on taxonomic and ecological attributes, including environment type (aquatic vs. terrestrial), voltinism, mean species body size, degree of SSD, and the direction of the size gradient.

METHODS

Data Collection

The data compilations of Horne *et al.* (2015; 2017; 2018) provide data on size-at-maturity responses to latitude, altitude and seasonal temperature change in a wide range of arthropod species, including marine, freshwater and terrestrial-living forms. Of these, we used only adult size measurements from studies where size responses for males and females had been reported separately. We were careful to ensure that we only included measurements when data for both sexes had been collected following the same protocol, and across the same study transect or time period. Body size measurements were for field-collected individuals only, and thus common garden studies were excluded. Adult sizes in these data sets have been quantified using a variety of metrics (lengths, volumes, and different mass types). These measurements were converted to dry mass (mg) using intra-specific regressions. Where these

were not available, we used regressions for closely related species, and occasionally more general inter-specific regressions. Our final data set consisted of 56 latitudinal-size clines representing 27 species, 129 altitudinal-size clines representing 50 species, and 144 seasonal temperature-size clines representing 52 species, examples of which are presented in Figure 1. All data and conversions are detailed in Data Set S1 in the Supporting Information.

To quantify changes in body size, the OLS slopes of $\log_e$ dry mass vs. latitude (^{o}), altitude (metres above sea level) and seasonal temperature (^{o}C) were used to examine clines in body size for single species, separated by sex. This exponential equation form has the advantage of being a better fit than alternate transformations (linear, quadratic and allometric), as judged by Akaike weights (Horne *et al.*, 2015; Horne *et al.*, 2017). In addition to fitting the empirical data well, this mathematical formulation is advantageous because it allows for an examination of relative size change and is unbiased by differences in absolute body size (also see Figure 1). To provide a measure of relative size change for each species and sex along each environmental gradient (latitude, season, altitude), we transformed the OLS slopes into percentage change in dry mass per ^{o}latitude, per ^{o}C of seasonal temperature change, and per 150m of elevation (approximating to a 1°C change (Anslow & Shawn, 2002)), respectively. The formula used was $(\exp^{(slope)} -1)*100$ = % change in mass per unit (Forster *et al.*, 2012). A negative percentage change indicates a decrease in size and a positive percentage change an increase. This allowed us to determine the relative difference in body size gradients between con-specific males and females (within single studies). Specifically, we used the degree of difference between male and female body size clines (% change in mass per unit) to calculate a *Size Cline Ratio*, such that:

Size Cline Ratio = (larger size cline / smaller size cline) - 1 (1)

This approach returns symmetrical results around zero, regardless of which sex has the greater response. We assigned this ratio a positive value when males had the greater response, and a negative value when the female response was greater. Given that we calculated body size clines using an exponential equation form, this metric provides a comparison of proportional body size change in males and females. This avoids the possible scaling effects encountered when using a linear regression, particularly in species with a high degree of SSD. For example, where both sexes exhibit the same proportional change in body size across environmental conditions, the slope of absolute size change would be greater in the larger sex. Were we to use a linear rather than exponential equation form, this would result in a *Size Cline Ratio* that differs from zero, despite no change in SSD.

Note that the *Size Cline Ratio* is derived from separate body size clines for males and females, and thus does not rely upon the body size of both sexes being measured at the exact same spatial or temporal point within a study (i.e. matched male-female values). An alternative size-scaling (allometric) approach, in which the $\log_{10}$ body size of one sex is plotted against that of the other (with the slope of an RMA regression then being derived), relies entirely on paired male and female body size data, which is not always obtained in ecological field studies. For this reason, we use the *Size Cline Ratio* as the dependent variable in our analyses, as we believe this to be a more complete representation of SSD patterns. Indeed, using the allometric approach reduced the amount of data available in comparison to the *Size Cline Ratio* method by ~60%. We repeated our analyses using an allometric approach, and summarise these findings, which largely support our conclusions, in the Supporting Information. We also utilise the allometric method in Table 1 to make direct comparisons with other published studies that have used this approach.

In addition to the *Size Cline Ratio*, we also used mean species body mass at the mid-latitude, mid-altitude or mid-temperature to calculate the absolute degree of SSD for each species

189 within single studies, using the Sexual Dimorphism Index (SDI) of Lovich and Gibbons (1992),
190 where:
191
192 SDI = (mass of larger sex / mass of smaller sex) - 1 (2)
193
194 We assigned this metric a positive value when males were the larger sex, and a negative
195 value when females were larger, thus providing a measure of the relative difference in size
196 between the sexes that varied symmetrically around zero. This allowed us to incorporate SDI
197 as an independent variable in subsequent statistical analyses.
198
199 *Statistical Analyses*
200 All statistical analyses were conducted in R (version 3.4.1) (R Core Team, 2014). For each of
201 the three major body size gradients, we compared several candidate models to best predict
202 within-species variation in the *Size Cline Ratio*. Using the *Size Cline Ratio* as the dependent
203 variable, we began by incorporating different taxonomic and ecological traits as fixed variables
204 in a global linear mixed effects model, created using the 'lmer' function in package lme4 (Bates
205 *et al.*, 2014). These included environment type (aquatic vs. terrestrial), voltinism (qualitative:
206 one generation or less vs. multiple generations per year), mean species body size (calculated
207 for females at the mid-latitude, mid-altitude and mid-temperature of each study), the direction
208 of the size gradient (negative or positive), and SDI (calculated in equation 2). Note that
209 voltinism was excluded when assessing seasonal temperature-size clines, as these
210 comprised of multivoltine species only. Species are related and therefore not statistically
211 independent, and our data set also included multiple *Size Cline Ratios* for the same species;
212 thus, we incorporated levels of taxonomic classification (class, order, family, and species) as
213 nested (hierarchical) random effects on the intercept to help control for phylogeny (Koricheva
214 *et al.*, 2013). Furthermore, given that the *Size Cline Ratio* was derived from data that varied
215 in their goodness of fit between studies and species, we weighted this metric based on

information quality (Koricheva *et al.*, 2013). Specifically, *Size Cline Ratios* were weighted by the inverse of the variance of the size cline slopes from which they were calculated. We recognise that our data set was derived from studies that adopted a population approach, in which the body size reported at a particular temperature, latitude or altitude is representative of a population mean rather than that of a single individual. Unfortunately, inconsistency between studies in the resolution of available data made it difficult to account for variation in information quality associated with each population mean. Nevertheless, it is noteworthy that we only included size clines from single studies, rather than combining size data from multiple studies that may vary greatly in their sampling protocol. Thus, within a cline, the number of individuals measured at each temperature, latitude or altitude should be reasonably consistent.

To examine which of our fixed variables best explained variation in the *Size Cline Ratio*, we generated a set of candidate models from all the possible combinations of the global model terms using the 'dredge' function in the 'MuMIn' package (Barton, 2017). Included in this candidate set was a null model, which contained no independent variables and predicted that the best estimate of the *Size Cline Ratio* was the intercept only. We compared the complete list of models using Akaike's Information Criterion (AIC), and the best model was identified as that with the lowest small-samples corrected AIC (AICc) (Burnham & Anderson, 2002). Using package 'AICcmodavg' (Mazerolle, 2014), we averaged over the whole set of candidate models (i.e. global model and all possible simpler models) to calculate the 'full' model-averaged coefficients for each of our fixed variables and determine their significance (z-statistic, $p<0.05$). The 'full' average makes the assumption that each variable is included in every candidate model, but in some models the corresponding coefficient (and its respective variance) is set to zero. This reduces the tendency of biasing the estimated coefficients away from zero. For each of the three major body size gradients, we used the intercept from the null model (i.e. constant mean model) to infer an overall weighted-mean *Size Cline Ratio*, which

accounted for the non-independence between species, as well as variation in information quality of the data. Finally, for each environmental cline we used an *F* test to determine whether the *Size Cline Ratio* differed significantly between taxonomic orders.

RESULTS

Latitudinal-Size Clines

Males exhibited stronger latitudinal-size clines relative to their conspecific females in 71% of cases. However, the overall weighted-mean *Size Cline Ratio* (1.62±1.66 95% CI), which accounted for the non-independence between species and variation in information quality, did not differ significantly from zero ($t_{5,23}$=1.95, p=0.06; Figure 2A). Consequently, neither of the sexes exhibited consistently greater proportional changes in body size than the other sex across latitude. The best-supported model for explaining variation in the *Size Cline Ratio* was a null model, which contained no independent variables and predicted that the best estimate of the *Size Cline Ratio* was the intercept (see Table S1 in Supporting Information). After model averaging, none of the fixed variables included in our global model could significantly explain variation in the *Size Cline Ratio* (see Table S7 for a summary of these outcomes). Neither did the *Size Cline Ratio* vary significantly between taxonomic orders ($F_{8,19}$=0.82, p=0.59). Note than when using the alternative allometric approach, on average males exhibited significantly greater proportional changes in body size than females across latitude. However, as with the *Size Cline Ratio*, none of the fixed variables included in our global model could significantly explain variation in the allometric slope between species (see Supporting Information).

Altitudinal-Size Clines

Females exhibited stronger altitudinal-size clines relative to their conspecific males in 56% of cases. The overall weighted-mean *Size Cline Ratio* (-0.96±2.22 95% CI) did not differ significantly from zero ($t_{5,50}$=-0.86, p=0.39; Figure 2B). Thus, neither of the sexes exhibited consistently greater proportional changes in body size than the other sex across altitude. The

best-supported model for explaining variation in the *Size Cline Ratio* was a null model, which contained no independent variables and predicted that the best estimate of the dependent variable was the intercept (see Table S3). After model averaging, none of the fixed variables included in our global model could significantly explain variation in the *Size Cline Ratio* (Table S7). Neither did the *Size Cline Ratio* vary significantly between taxonomic orders ($F_{8,46}$=0.11, p=0.99). These outcomes are also corroborated by analysis using the alternative allometric approach (see Supporting Information).

Seasonal Temperature-Size Clines

Females exhibited stronger seasonal temperature-size clines relative to their conspecific males in 61% of cases. The overall weighted-mean *Size Cline Ratio* (0.17±0.97 95% CI) was not significantly different from zero ($t_{5,66}$=0.34, p=0.73; Figure 2C). Thus, neither of the sexes exhibited consistently greater proportional changes in body size than the other sex with seasonal warming. The best-supported model for explaining variation in the *Size Cline Ratio* was a null model, which contained no independent variables and predicted that the best estimate of the dependent variable was the intercept (see Table S5). After model averaging, none of the fixed variables included in our global model could significantly explain variation in the *Size Cline Ratio* (Table S7). There was no significant difference in the *Size Cline Ratio* between taxonomic orders ($F_{7,63}$=0.44, p=0.87). These outcomes were corroborated by analyses using the alternative allometric approach (see Supporting Information).

Additional Observations and Considerations

For each of the environmental-body size clines, there were some particularly strong *Size Cline Ratios*. Given that the body size cline of the less variable sex can be zero (i.e. the denominator in equation 1), theoretically the *Size Cline Ratio* can be infinite. Thus, a very low denominator value compared with the numerator can generate very large ratios. Therefore, we also calculated the overall weighted-mean *Size Cline Ratio* for each environmental cline when

these strong outliers were excluded. Specifically, we excluded *Size Cline Ratios* that ranged above and below 1.5x the interquartile range. This resulted in the removal of 3, 14 and 11 outliers from latitudinal-, altitudinal-, and seasonal temperature-size clines respectively. As before, the mean *Size Cline Ratio* for both altitudinal-size clines (0.10±0.33 95% CI) and seasonal temperature-size clines (-0.09±0.10 95% CI) did not differ significantly from zero ($t_{6,35}$=0.57, p=0.59 and $t_{6,54}$=-1.74, p=0.09 respectively). When these outliers for latitudinal-size clines were excluded, the mean *Size Cline Ratio* became significantly positive (0.38±0.29 95% CI; $t_{5,20}$=2.66, p=0.01), suggesting greater variation in male than female body size with latitude.

Across all three major body size gradients, there were a small number of cases (n=18) where the direction of the size gradients differed between males and females within a species (i.e. whereas one sex increased in size, the other decreased in size). Yet in each case, the slope of at least one of these paired size gradients, and in most cases both (n=14), did not differ significantly from zero (determined by the 95%CIs overlapping with zero). Thus, we find strong and consistent evidence that within a species, males and females share the same sign (positive or negative) in the environmental-body size clines we have tested.

DISCUSSION

To our knowledge, this study provides the largest quantitative comparison of male and female biogeographical and temporal (seasonal) body size gradients to date in arthropods, including marine, freshwater and terrestrial species. Given the contrasting outcomes from recent studies investigating sex-specific body size plasticity under laboratory conditions (Table 1), we combined body size data from multiple species and studies to provide a field-based comparison to these earlier findings.

Blanckenhorn *et al.* (2006) previously compared latitudinal-size clines between males and females in vertebrates and invertebrates, finding that the different metrics used to quantify

variation in SSD led to contrasting outcomes. Males were the more variable sex when the ratios of sex-specific latitudinal slopes (i.e. *Size Cline Ratio*) were compared, but neither sex was more variable when an allometric approach was used (Blanckenhorn *et al.*, 2006). In our assessment of latitudinal-size clines, males exhibited greater L-S clines than females in over two thirds of our data set, and after removing particularly strong outliers, the weighted-mean *Size Cline Ratio* was significantly greater than zero, indicating greater variability in male than female body size across latitude. Moreover, this same pattern was evident following analysis using the allometric approach (see Supporting Information). However, we note that this allometric approach (which relies upon paired male and female values) reduced the amount of latitudinal-body size data available by almost two thirds.

Of the three environmental gradient types examined, latitudinal-size clines are the most likely to include not just phenotypically plastic effects, but also genetic differences between populations. Evidence of greater variability in male than female size against latitude is consistent with the hypothesis that, over evolutionary time, directional selection has acted more strongly on male than female size (Fairbairn, 1997). This hypothesis may be developed further, given that a large proportion of our latitudinal-size clines were for Lepidoptera, many of which exhibit protandry (i.e. earlier male emergence) and show converse latitudinal-size clines, decreasing in size towards the poles. This finding therefore supports the suggestion that, due to seasonal time constraints at higher latitudes, particularly strong selection for earlier male emergence (and thus smaller size) may be driving greater variability in male than female body size across latitudinal gradients, providing a possible explanation for the observed patterns (Roff, 1980; Blanckenhorn *et al.*, 2007b).

In contrast to latitudinal gradients, altitudinal-size clines and seasonal temperature-size clines are somewhat less likely to be influenced by genetic differences between populations and more so by phenotypic plasticity. Indeed, we find that neither of the sexes exhibit consistently

greater proportional changes in body size than the other sex across altitudinal and seasonal gradients, akin to earlier findings reported for plastic temperature-size responses measured in the laboratory (Hirst *et al.*, 2015). Although changes in juvenile density and food quantity/quality have been shown to produce greater female size plasticity within arthropod species (Stillwell *et al.*, 2010), the environmental gradients we examine here are strongly characterized by predictable variation in temperature, whereas gradients in other variables such as food quality and juvenile density are relatively less predictable. Furthermore, whereas Rohner *et al.* (2018) found that the larger sex generally exhibited greater plasticity in response to environmental factors in insects (including food quantity and temperature), variation in the *Size Cline Ratio* in our study could not be explained by any combination of taxonomic and ecological traits, including the magnitude and direction of SSD. Therefore, we find no evidence to suggest that body size plasticity is generally greater in the larger sex.

A tentative explanation for the lack of systematic differences between male and female altitudinal and seasonal body size gradients may lie in their ontogenetic establishment, particularly if these environmental clines are primarily the result of body size plasticity in response to developmental temperature. A meta-analysis investigating the proximate cause of sexual size dimorphism in insects concluded that in many species (79%), the larger sex also had a longer larval development time (Teder, 2014). Furthermore, greater differences in larval development time between the sexes corresponded with a greater degree of SSD in a diverse range of insect clades (Teder, 2014). These findings suggest that prolonged development time in the larger sex plays an important role in establishing SSD, although differences in the growth rate of males and females has also been proposed as the primary mechanism (Blanckenhorn *et al.*, 2007a). We may predict that the later developing sex would exhibit stronger body size clines if we make two assumptions. First, SSD arises primarily from longer development time in the larger sex, whether this be through prolonged development of several consecutive instars (Tammaru *et al.*, 2010), or through the addition of an extra instar

at the end of ontogeny (Esperk & Tammaru, 2006). Second, temperature-size responses are established gradually over ontogeny, such that eggs show little or no response and the strength of the response accumulates over time (Forster *et al.*, 2011). Furthermore, we would expect a stronger *Size Cline Ratio* in those species with a higher degree of SSD. Yet, we do not observe such patterns. This mis-match between prediction and observation may arise because the second assumption appears not to hold, at least in those few arthropods studied (Forster & Hirst, 2012; Horne *et al.*, 2019). The temperature-size responses of these species show no consistent change (strengthening or weakening) during the second half of ontogeny (Forster & Hirst, 2012; Horne *et al.*, 2019). If the ontogenetically early onset of body size-clines is widespread among arthropods, this may explain why both sexes show a similar degree of plasticity in adult size, even if the larger sex has a markedly longer development time. In contrast, the effects of other environmental variables such as food quality/quantity may continue to accumulate across the whole of ontogeny. Our speculative proposal for such differences requires further empirical examination and testing.

Although we find no systematic patterns in the *Size Cline Ratio* across altitudinal and seasonal gradients, considerable variation exists in this metric between species (Figure 2). Although it is difficult to conduct a detailed assessment of the life history, physiology and population dynamics of every species in our data set, we make two suggestions to improve understanding. First, rather than treating body size as an isolated trait, further studies should incorporate co-adaptation of responses to the environment (Angilletta Jr *et al.*, 2006). Specifically, differences in body size at maturity can arise from differences in growth, development rates (e.g. affecting protandry), or both, and all these traits will be selected according to their influences on and by the schedules of mortality and reproduction (e.g. fecundity potential) (Roff, 1986; Marshall & White, 2018). Thus, we advocate treating life-history differences between the sexes as a co-adapted whole, and identifying specific environmental (including social) conditions that generate these differences. Second, particular

405 case studies may help elucidate the patterns (or lack thereof) in SSD across environmental
406 gradients. For example, considerable variation exists in the *Size Cline Ratio* across altitudinal
407 gradients within the Orthoptera. Of these, data for *Chorthippus cazurroi*, *C. parallelus* and *C.*
408 *yersini* were derived from Laiolo *et al.* (2013), who investigated intra-specific variation in SSD
409 in mountain grasshopper communities. C. *yersini* exhibits a particularly strong negative *Size*
410 *Cline Ratio* (i.e. greater variability in female size; Figure 2B). As the authors point out, this may
411 be explained by the fact that females of a phylogenetically similar species produce additional
412 instars when raised at higher temperatures and with higher food quality (Hassall & Grayson,
413 1987). Prolonged development through the addition of extra instars during ontogeny would
414 allow females to become substantially larger than males in favourable conditions, and thus
415 could provide a proximate explanation for the greater variation in female than male size
416 observed across altitude in this species (Laiolo *et al.*, 2013). In contrast, *C. parallelus* exhibits
417 a very strong positive *Size Cline Ratio* (i.e. greater variability in male size; Figure 2B) and is
418 one of the few species in the *Chorthippus genus* for which females cannot alter the number of
419 instars during development (Schädler & Witsack, 1999). This fixed instar number may act to
420 constrain variability in female body size across altitudinal gradients; hence the observations
421 of Laiolo *et al*. 2013. Other studies have also identified sex-biased plasticity in the
422 physiological mechanisms controlling insect body size during ontogeny, including the
423 hormonal pathways regulating growth rate and critical size (Davidowitz *et al.*, 2004; Stillwell &
424 Davidowitz, 2010; Testa *et al.*, 2013; Nijhout *et al.*, 2014; Stillwell *et al.*, 2014). However, the
425 mechanism(s) leading to variation in male and female body size responses are unlikely to be
426 universal, particularly as these plastic size responses are not just limited to arthropods
427 (Atkinson, 1994; Blanckenhorn *et al.*, 2006; Forster *et al.*, 2012).
428
429 The data presented here represents only a small fraction of all arthropod species, with some
430 taxa better represented than others. Furthermore, variation in abiotic and biotic conditions
431 across environmental gradients will undoubtedly vary between study locations, further

confounding any potential patterns. Ultimately, if we are to make more broad-scale predictions about sex-based differences in response to the environment, we require a more detailed understanding of the underlying selective pressures driving clines in body size. Such understanding will provide a more comprehensive hypothesis-driven approach to explaining biogeographical and temporal variation in SSD.

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DATA ACCESSIBILITY

Raw data used in this study are available in Supporting Information Data Set S1.

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603

Table 1. Comparison of sex-specific plasticity in body mass in relation to environmental variables. We followed the methodology of Stillwell *et al.* (2010), such that $\log_{10}$ male size is plotted on the y-axis, and $\log_{10}$ female size on the x-axis. Hence when the RMA slope is <1 females are the more size responsive sex, and when the RMA slope is >1 males are more size responsive. CV is the coefficient of variation of body size across the data within each study. Asterisks denote a significant difference between the sexes, where * gives p<0.05, and ** gives p<0.01. Table modified from Stillwell *et al*. (2010), with additions from Blanckenhorn *et al.* (2006) (which includes common garden experimental data), Hirst *et al*. (2015), and this study.

Environmental Variable (Taxonomic group)	**Which Sex is More Plastic?**			**Average degree of plasticity (CV among environments)**			**Source**
	Females (No. studies with RMA slope < 1)	**Males (No. studies with RMA slope > 1)**	X^2	**Female**	**Male**	***t***	
Field-based clines:							
Latitude (Arthropoda)	8 (32.0%)	17 (68.0%)	2.56	15.3%	17.2%	-1.81	This study
Altitude (Arthropoda but primarily Insecta)	32 (57.1%)	24 (42.8%)	0.88	12.0%	11.5%	0.58	This study
Seasonal Temperature (Arthropoda but primarily Crustacea)	40 (60.6%)	26 (39.4%)	2.56	21.9%	19.7%	2.67**	This study
Latitude (Arthropoda)	17 (44.7%)	21 (55.3%)	0.24	5.50%	5.54%	0.27	Blanckenhorn *et al.* (2006)
Controlled laboratory-based clines:							
Temperature (Arthropoda)	55 (47.4%)	61 (52.6%)	0.22	12.3%	12.1%	0.41	Hirst *et al*. (2015)
Temperature (Insecta)	46 (48.9%)	48 (51.1%)	0.01	11.6%	11.0%	1.14	Hirst *et al*. (2015)
Larval density / larval competition / diet quantity (Insecta)	18 (72.0%)	7 (28.0%)	4.84*	16.0%	12.2%	3.42**	Stillwell *et al*. (2010)
Pathogenic infection (Insecta)	3 (50.0%)	3 (50.0%)	0.00	6.9%	7.2%	0.34	Stillwell *et al*. (2010)
Photoperiod (Insecta)	1 (16.7%)	5(83.3%)	2.67	8.6%	10.7%	2.18	Stillwell *et al*. (2010)
Diet Quality (Insecta)	83 (61.9%)	51 (39.1%)	7.64**	12.5%	11.5%	2.47*	Stillwell *et al*. (2010)

FIGURE LEGENDS

Figure 1. Examples of male (closed circles) and female (open triangles) body size-clines across latitude (A, B), altitude (C, D) and with seasonal temperature variation (E, F). Left-hand panels show absolute changes in dry mass (mg), whilst right-hand panels show changes in natural log (ln) of dry mass, and thus relative change in body size. L-S data (A, B) is for *Dalbulus maidis* (Hemiptera), adapted from de Oliveira *et al.* (2004); A-S data (C, D) is for *Omocestus viridulus* (Orthoptera), adapted from Berner and Blanckenhorn (2006); seasonal temperature-size data (E, F) is for *Paracerceis sculpta* (aquatic Isopoda), adapted from Shuster and Guthrie (1999). Dashed grey line indicates seasonal variation in temperature in panel E. Note that males of *Paracerceis sculpta* coexist as three genetically distinct adult morphs; in panels E and F we show data for y-males, which mature most rapidly and are the smallest morph, resulting in particularly strong sexual size dimorphism. Despite the high degree of SSD, females and y-males exhibit very similar proportional changes in body size with seasonal warming (panel F). This highlights the importance of using an exponential equation form to compare body size-clines, which avoids the scaling effects associated with using a linear regression, particularly in species with a high degree of SSD.

Figure 2. *Size Cline Ratios* for **A)** latitudinal-size (L-S) clines (n=28), **B)** altitudinal-size (A-S) clines (n=64) and **C)** seasonal temperature-size (T-S) clines (n=72) for the arthropod species included in this study, categorized by taxonomic order. The horizontal dashed line denotes zero, i.e. no difference between male and female body size responses. Values greater than zero indicate more responsive male mass. Values less than zero indicate more responsive female mass. The overall weighted-mean *Size Cline Ratio* (±95% CI) is also shown for each environmental cline.

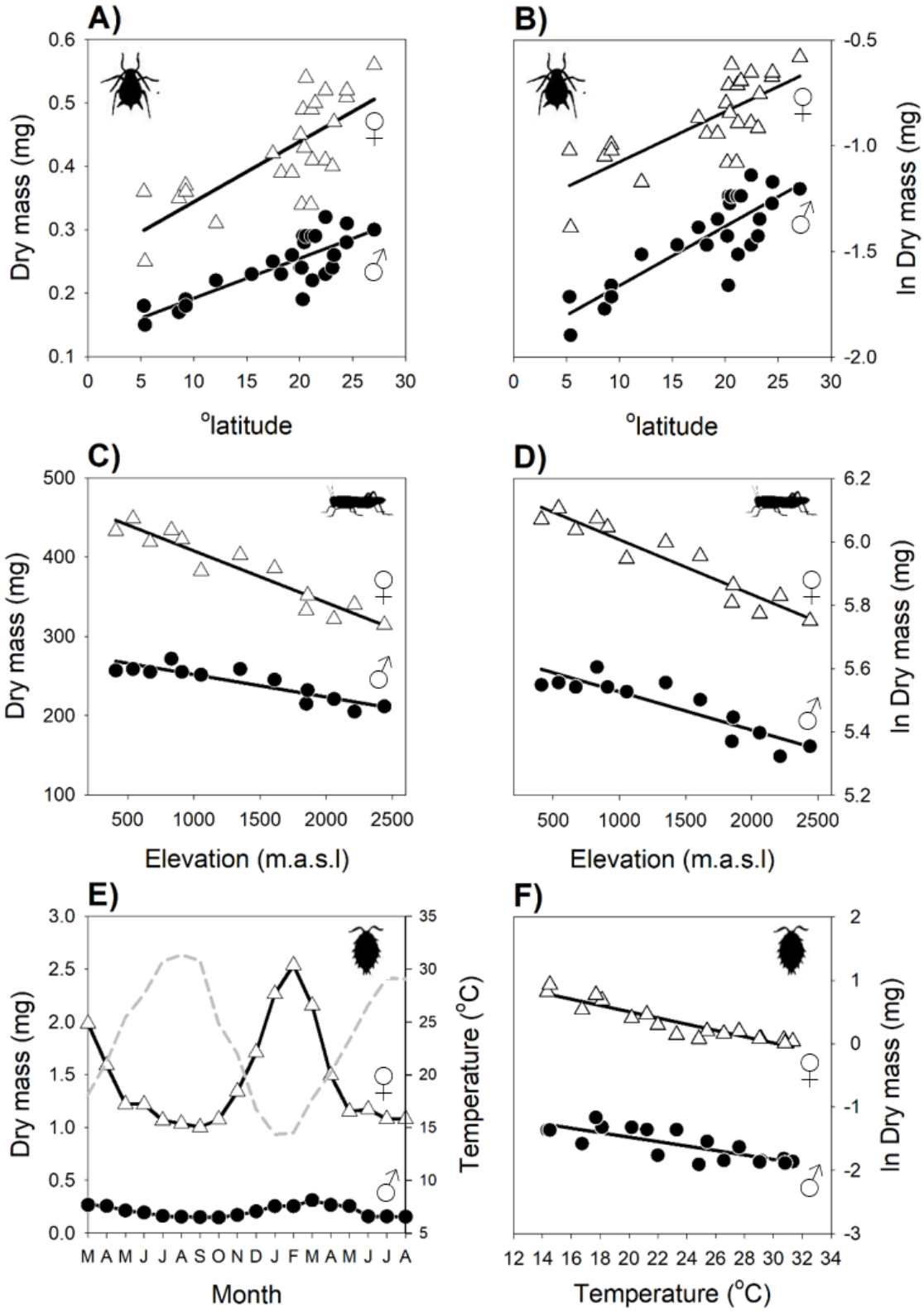
A)
B)
C)
D)
E)
F)
Dry mass (mg)
ln Dry mass (mg)
°latitude
Elevation (m.a.s.l)
Temperature (°C)
Month
M A M J J A S O N D J F M A M J J A

Figure 1

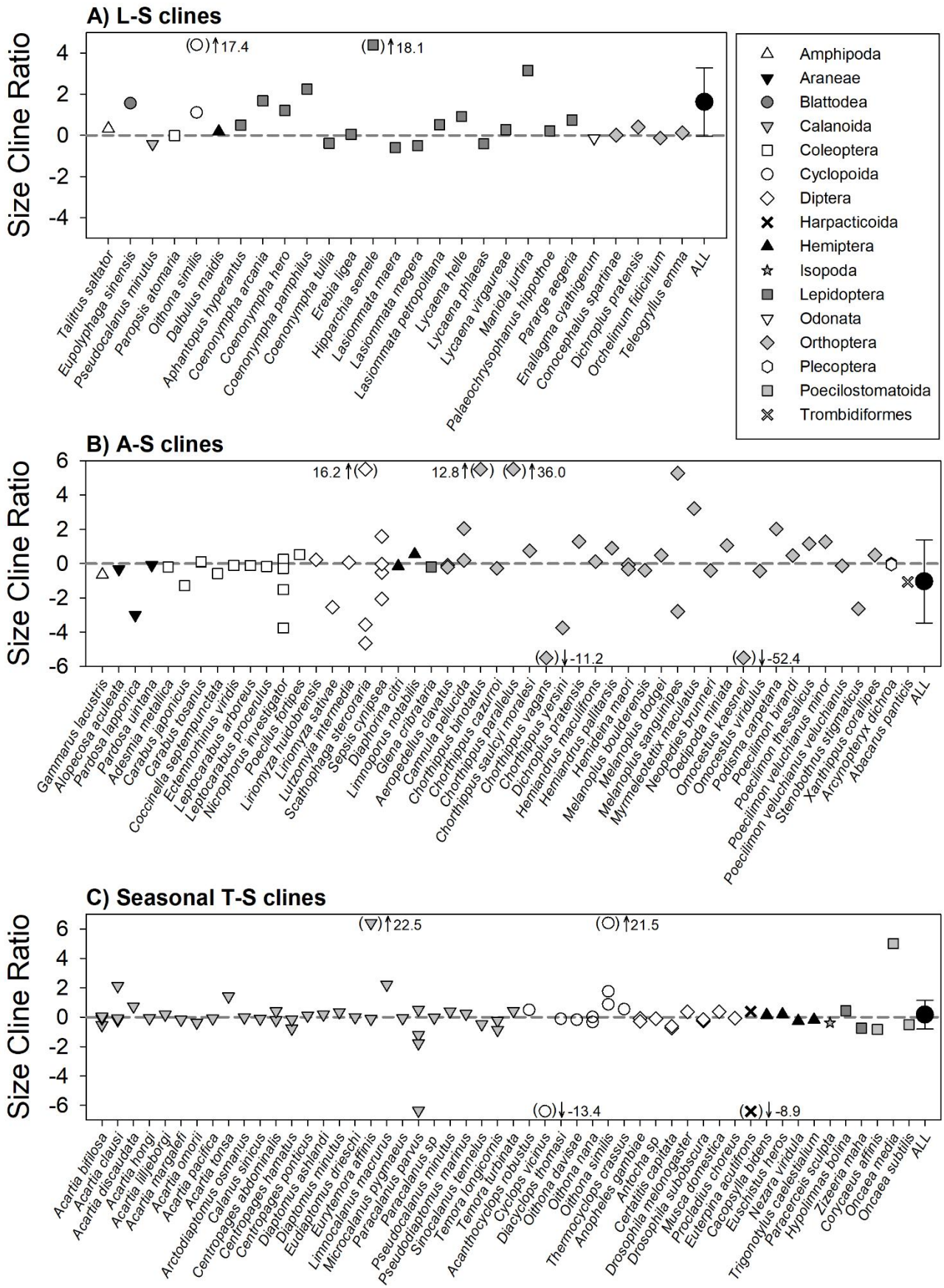
A) L-S clines
Size Cline Ratio
(○)↑17.4
(■)↑18.1
Amphipoda
Araneae
Blattodea
Calanoida
Coleoptera
Cyclopoida
Diptera
Harpacticoida
Hemiptera
Isopoda
Lepidoptera
Odonata
Orthoptera
Plecoptera
Poecilostomatoida
Trombidiformes
Talitrus saltator
Eupolyphaga sinensis
Pseudocalanus minutus
Paropsis atomaria
Oithona similis
Dalbulus maidis
Aphantopus hyperantus
Coenonympha arcania
Coenonympha hero
Coenonympha pamphilus
Coenonympha tullia
Erebia ligea
Hipparchia semele
Lasiommata maera
Lasiommata megera
Lasiommata petropolitana
Lycaena helle
Lycaena phlaeas
Lycaena virgaureae
Maniola jurtina
Palaeochrysophanus hippothoe
Pararge aegeria
Enallagma cyathigerum
Conocephalus spartinae
Dichroplus pratensis
Orchelimum fidicinium
Teleogryllus emma
ALL
B) A-S clines
Size Cline Ratio
16.2↑(◇)
12.8↑(◆)
(◆)↑36.0
(◆)↓-11.2
(◆)↓-52.4
Gammarus lacustris
Alopecosa aculeata
Pardosa lapponica
Pardosa uintana
Adesmia metallica
Carabus japonicus
Carabus tosanus
Coccinella septempunctata
Ectemnorhinus viridis
Leptocarabus arboreus
Leptocarabus procerulus
Nicrophorus investigator
Poecilus fortipes
Liriomyza huidobrensis
Liriomyza sativae
Lutzomyia intermedia
Scathophaga stercoraria
Sepsis cynipsea
Diaphorina citri
Limnoporus notabilis
Glena cribraria
Aeropedellus clavatus
Camnula pellucida
Chorthippus binotatus
Chorthippus cazurroi
Chorthippus parallelus
Chorthippus saulcyi moralesi
Chorthippus vagans
Chorthippus yersini
Dichroplus pratensis
Hemiandrus maculifrons
Hemiandrus pallitarsis
Hemideina maori
Melanoplus boulderensis
Melanoplus dodgei
Melanoplus sanguinipes
Myrmeleotettix maculatus
Neopedies brunneri
Oedipoda miniata
Omocestus kaesneri
Omocestus viridulus
Podisma carpetana
Poecilimon birandi
Poecilimon thessalicus
Poecilimon veluchianus minor
Poecilimon veluchianus veluchianus
Sterobothrus stigmaticus
Xanthippus coralipes
Arcyptera dichroa
Abacarus panticis
ALL
C) Seasonal T-S clines
Size Cline Ratio
(▽)↑22.5
(○)↑21.5
(○)↓-13.4
(✕)↓-8.9
Acartia bifilosa
Acartia clausi
Acartia discaudata
Acartia hongi
Acartia tiljeborgi
Acartia margalefi
Acartia omorii
Acartia pacifica
Acartia tonsa
Arctodiaptomus osmanus
Calanus sinicus
Centropages abdominalis
Centropages hamatus
Centropages ponticus
Diaptomus ashlandi
Diaptomus minutus
Eudiaptomus drieschi
Eurytemora affinis
Limnocalanus macrurus
Microcalanus pygmaeus
Paracalanus parvus
Paracalanus sp
Pseudocalanus minutus
Pseudodiaptomus marinus
Sinocalanus tennelus
Temora longicornis
Temora turbinata
Acanthocyclops robustus
Cyclops vicinus
Diacyclops thomasi
Oithona davisae
Oithona nana
Oithona similis
Thermocyclops crassus
Anopheles gambiae
Antocha sp
Certatitis capitata
Drosophila melanogaster
Drosophila subobscura
Musca domestica
Procladius choreus
Euterpina acutifrons
Cacopsylla bidens
Euschistus heros
Nezara viridula
Trigonotylus caelestialium
Paracercelis sculpta
Hypolimnas bolina
Zizeeria maha
Corycaeus affinis
Oncaea media
Oncaea subtilis
ALL

Figure 2